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THE REDISCOVERY OF A MALAGASY ENDEMIC: *TAKHTAJANIA PERRIERI* (WINTERACEAE)[1]

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ABSTRACT

The history and rediscovery of *Takhtajania perrieri* (Capuron) Baranova & J.-F. Leroy, the only extant representative of the primitive family Winteraceae in the Africa/Madagascar region, is recounted.

Key words: discovery, Madagascar, *Takhtajania*, Winteraceae.

For most of the 20th century, *Takhtajania perrieri* (Capuron) Baranova & J.-F. Leroy stood as the Holy Grail of Malagasy botany. Numerous expeditions searched in vain for the only possible living member of the ancient family Winteraceae in the Africa–Madagascar region at the Manongarivo Special Reserve in northwestern Madagascar, where, in 1909, Henri Perrier de la Bâthie collected the only known specimens. With hundreds of square kilometers of intact forest protected within the Manongarivo reserve, the species must surely still exist there! Nevertheless, the dozens of botanists who ascended the slopes of Mt. Antsatrotro to the 1700-meter elevation cited on Perrier de la Bâthie's handwritten labels, passing through what is infamously acknowledged to be the most dense zone of terrestrial leeches in all of Madagascar, have all failed to relocate *Takhtajania*.

By the spring of 1997, I commenced work on the *Generic Tree Flora of Madagascar* (Schatz, in press). The *Tree Flora* will serve as a revision and expansion of René Capuron's 1957 *Essai d'Introduction à l'Etude de la Flore Forestière de Madagascar*, a work existing only in mimeographed

[1] At the Missouri Botanical Garden, I thank P. H. Raven and P. P. Lowry II for the opportunity to study the Malagasy flora, and V. Hollowell and P. P. Lowry II for helpful comments on the manuscript. In Paris, Ph. Morat and his staff have always extended the most cordial hospitality during my visits to the Laboratoire de Phanérogamie. In Madagascar, fieldwork was conducted under collaborative agreements between the Missouri Botanical Garden and the Parc Botanique et Zoologique de Tsimbazaza and the Direction de la Recherche Forestière et Piscicole, FOFIFA, Antananarivo, Madagascar. Fieldwork would have been impossible without the assistance of the World Wide Fund for Nature; special thanks go to Jean Marc Garreau and Désiré Ravelonarivo at their Andapa office. I gratefully acknowledge courtesies extended by the Government of Madagascar (Direction Générale de la Gestion des Ressources Forestières) and by the Association Nationale pour la Gestion des Aires Protégées. This research was conducted with support from U.S. National Science Foundation grants DEB-9024749 and DEB-9627072, and grants from the National Tropical Botanical Garden, Kauai, and the National Geographic Society.

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form. Although it would be another six years before he described *Bubbia perrieri* [= *Takhtajania perrieri*] (Capuron, 1963), by 1957 Capuron had already determined that *Perrier de la Bâthie 10158* constituted the first and only record of the family Winteraceae in Madagascar, including a description of the family in his *Essai,* as represented in Madagascar by "Un seul genre et une seule espèce: Bubbia Perrieri R. Cap." (p. 96), with the further note that "La famille est nouvelle pour Madagascar; l'espèce provient du massif du Manongarivo" (p. 104). In Paris during March of 1997, I decided to write the description of *Takhtajania* for the *Tree Flora,* and, that to do so, it was high time that I examine the type specimen. After several inquiries, two sheets of *Perrier de la Bâthie 10158* were located in the office of Thierry Deroin. He, with the late Jean-François Leroy (1915–1999), had recently studied the vasculature of the ovary utilizing the type material (Deroin & Leroy, 1993). Over the course of several days as I wrote my generic description, I stared periodically at those enigmatic specimens collected nearly 90 years earlier. While wondering whether the species might still exist, I had to conclude my treatment of the genus with the unsatisfactory statement that despite numerous attempts, *Takhtajania* had not been seen again. Two months later, back in St. Louis, with the images of those type specimens still very fresh in my mind's eye, I opened the enfolding newspapers of a collection tentatively determined as "Rhamnaceae," made in 1994 from the Anjanaharibe-Sud Special Reserve by the Malagasy collector Fanja Rasoavimbahoaka, and, eureka, there it was! In an instant, I realized that *Takhtajania* had indeed been seen again, but not where we had been looking for it. Set into motion that momentous day were a series of events culminating in the following papers.

From "Indet." To Political Cartoon: One Species' History

The first documented human contact with *Takhtajania* occurred in May 1909 on the Manongarivo Massif in northwestern Madagascar, a chance event preserved for all time as two herbarium specimens (*Perrier de la Bâthie 10158*) deposited at the Muséum Nationale d'Histoire Naturelle in Paris. Both Capuron (1963) and Leroy (1978, 1993) transcribed the locality data on Perrier de la Bâthie's handwritten label as "Massif du Manongarivo, au bord des ruisseaux, sur schistes liasiques, vers 1,700 m d'altitude." It seems likely, however, that Perrier de la Bâthie's altimeter was inaccurate, insofar as he attributed some of his collections from the same trip to 2000 m, despite a maximum altitude for the massif of 1876 m at the summit of Mt. Antsatrotro. Given this, and that *Takhtajania* is now known to range from 1100 to 1550 m altitude at its second known locality within the Anjanaharibe-Sud Special Reserve, this may partially explain why it has never been relocated at Manongarivo: we may well have been looking for it at too high an elevation! Accompanying the two type sheets enclosed within a red Type folder are Perrier de la Bâthie's field notes. These were reproduced in full by Leroy (1978), and reveal that *Takhtajania* first entered our collective botanical consciousness as a "family indet."; based upon its leaf, stamen, and ovary characteristics, Perrier suggested both "Annonaceae?" and "Dilleniaceae? (*Tetracera*)," believing the single carpel to correspond to a carpel of a flower with multiple, free carpels. A later annotation (with a preprinted partial date of "193 ," the specific year left blank) affixed to one of the sheets by J. Ghesquière, a specialist in Annonaceae, rejected it from that family by noting simply "Magnol.," perhaps as an ordinal placement. Leroy (1978) cited undated notes referring to the winteraceous genera *Bubbia* and *Drimys* by H. Humbert; although he may have been the first to recognize the correct family placement, these notes no longer accompany the type specimens. Nevertheless, *Takhtajania* remained nameless for 54 years until Capuron (1963) formally described it as *Bubbia perrieri.* Such a lag time between field collection and its actual description serves as a useful illustration of the occasionally slow pace of botanical studies.

Having finally received a name, *Bubbia perrieri* soon became the focus of additional studies on pollen (Straka, 1963; Lobreau-Callen, 1977) and leaf anatomy (Baranova, 1972; Bongers, 1973). These studies reported colpate or trichotomocolpate (trichotomosulcate) pollen apertures and an anomocytic stomatal cell arrangement, both features anomalous within the Winteraceae (neither condition is corroborated herein by Keating or Sampson, respectively). Stimulated by these novel findings, Leroy (1977) expanded upon Capuron's observation of a bilobed stigma for *Bubbia perrieri,* and daringly hypothesized a compound unilocular ovary comprised of two united carpels; he also presciently suggested a close alliance to Canellaceae. For Leroy (1978), such radical differences clearly merited distinct higher-taxon status, and thus a new genus was described. *Bubbia perrieri* Capuron became *Takhtajania perrieri* (Capuron) Baranova & J.-F. Leroy, and the new genus became the type of a wholly new subfamily Takhtajanioideae. When

Vink's (1978) studies of the ovary concurred with his bicarpellate hypothesis, Leroy felt sufficiently vindicated against Tucker and Sampson's (1979) cautionary skepticism in the journal *Science* that his enthusiasm knew no bounds. In 1980, he raised his subfamily Takhtajanioideae to the rank of family: Takhtajaniaceae, indeed, from a "family indet." to a family apart!

Meanwhile, numerous botanists failed to relocate *Takhtajania* at the Manongarivo Special Reserve. Capuron collected there extensively in 1954, including the upper slopes of Mt. Antsatrotro, but then he apparently never returned. In 1966, he stayed closer to the main road from Maromandia to Ambanja that passes ca. 10 km to the west of the Reserve boundary, and fully 25 km west of the upper slopes of Antsatrotro. Vink (1978) recounted that Capuron told him that the type locality was completely deforested, a curious remark given the vast area of intact forest present still today (Gautier et al., 1999). Several years later, Josef Bogner (M) searched for Araceae on the southern slopes of Antsatrotro north of Bejofo, and the late Al Gentry walked in from the road to as high as 300 m altitude in 1974. Then, at the behest of Leroy, Raymond Rabevohitra (TEF) once again searched the upper slopes of Antsatrotro in 1979, but found no trace of *Takhtajania*. Beginning in May of 1989 (Schatz, 1989), the Missouri Botanical Garden has conducted numerous expeditions to Manongarivo, and since 1994, Laurent Gautier (1997, 1999) has headed Geneva's ongoing inventory efforts there. For all who made the arduous pilgrimage to Manongarivo, *Takhtajania* would remain elusive.

Some 150 km to the southeast of Manongarivo, also in 1994, Fanja Rasoavimbahoaka began work as a local collector at the Marojejy Strict Nature Reserve (now a national park) and Anjanaharibe-Sud Special Reserve in conjunction with an AN GAP (the National Association for the Management of Protected Areas)/World Wide Fund for Nature protected areas project. That May, he ascended a trail used by local gem and crystal hunters leading west from the abandoned village of Andranotsarabe, which had served as a camp, gravel depository, and water source during the building of the road connecting Andapa and Bealanana that bisects the Anjanaharibe-Sud Reserve. Unbeknownst to him, he collected *Takhtajania* in flower (Fig. 1; additional images of *Takhtajania* may be found on the web at http://www.mobot.org/MOBOT/Madagasc/winterac.html), exactly 85 years to the month after Perrier de la Bâthie's original collection from Manongarivo. Later that same year, a multi-disciplinary study of altitudinal variation, sponsored by WWF and headed by Steve Goodman (1998), used this same trail to access the summit of Anjanaharibe-Sud. In fact, they established their 1200-m "Camp 2" right amidst the *Takhtajania* population. Expedition botanist Désiré Ravelonarivo collected fruiting *Takhtajania* both in September and November, and all of the expedition members must have walked by *Takhtajania* numerous times along the trail.

This brings us forward to that fateful day in May 1997, when I opened the newspapers containing *F. Rasoavimbahoaka 303*. The first person to whom I showed the collection was Peter H. Raven, who had launched MBG's activities in Madagascar several decades earlier, partly in hopes of finding *Takhtajania* again. He suggested that I immediately prepare an announcement of the rediscovery for the journal *Nature* (Schatz et al., 1998). I then dispatched e-mails to Paris and Madagascar, sounding the call to action. Several weeks later, members of our Malagasy staff including Sylvie Andriambololonera, Jeannie Raharimampionona, and Pierre Jules ("Coca") Rakotomalaza accompanied Désiré back to the *Takhtajania* locality at Anjanaharibe-Sud, photographing its flowers and collecting the first lot of specialized research materials that would be utilized in the following new studies. The following month, a specimen for the Komorov Institute in St. Petersburg was presented to Armen Takhtajan at a special birthday celebration for him in St. Louis; born just one year after Perrier de la Bâthie first collected *Takhtajania*, he had waited 87 years for its rediscovery.

Since then, *Takhtajania* has been revisited numerous times. The journey from Andapa to Andranotsarabe by 4-wheel-drive vehicle takes three hours, if it has been relatively dry the previous days. However, subjected to over 3600 mm of rainfall per year, portions of the road are deteriorating rapidly, and landslides threaten continued access to the population. Having arrived at the trailhead, one must gently climb little more than 200 m in elevation through beautiful forest. Even when it is raining—which it often is—the leech population does not even begin to compare with that of the slopes of Mt. Antsatrotro at Manongarivo. In less than an hour, one enters *Takhtajania*'s realm, the narrow, flattened ridges followed by the trail, and the uppermost portions of the steep slopes falling away on either side of the ridges. With its large, glossy, dark green leaves clustered toward the apex of vertical stems, *Takhtajania* stands out in the understory, its slender trunk often leaning severely after surviving the impact of fallen debris. Extending over eleven square kilometers, this second recorded *Takhtajania* population appears to be thriv-

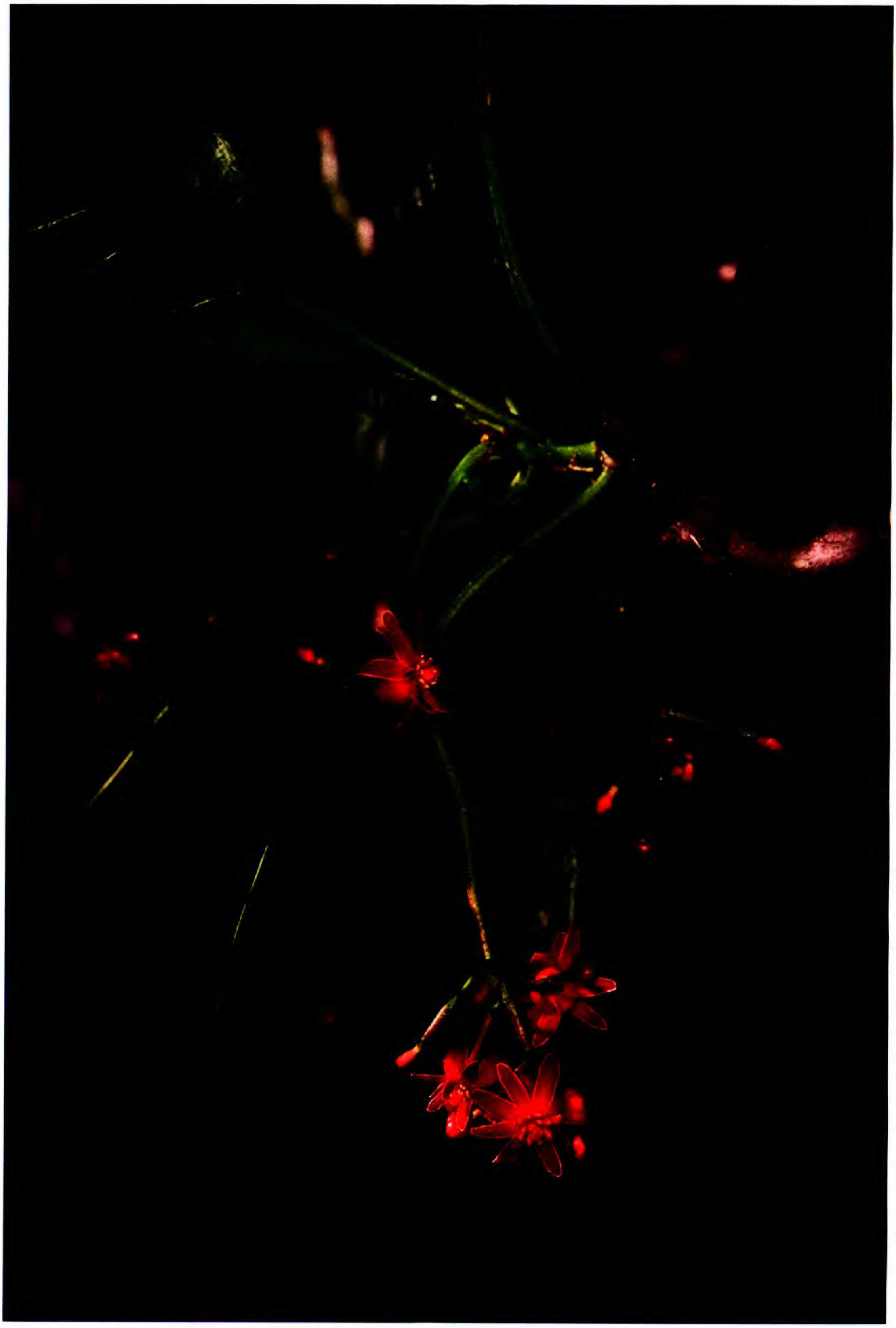

Figure 1. Flowering branch of *Takhtajania perrieri* (Capuron) Baranova & J.-F. Leroy at the Anjanaharibe-Sud Special Reserve, Madagascar.

ing; Birkinshaw and colleagues (1999a) have estimated a minimum of 42,020 individuals representing all size classes, including abundant seedlings.

In his 1998 New Year's address to representatives of the diplomatic community, the President of Madagascar, Didier Ratsiraka, heralded *Takhtajania* as a national treasure that dated back to the time of the dinosaurs. His remarks immediately drew the attention of other national figures. Ministers, at that time, of the Environment, and Waters and Forests, C. Vaohita and R. Rajonhson, respectively, accompanied by the Directors of Biodiversity Valorization, and Ecotourism at ANGAP, M. Faramalala and J. Rakotoarisoa, respectively, all made the long trek to see *Takhtajania.* Shortly thereafter, a political cartoon appeared in one of the daily Antananarivo newspapers depicting a Malagasy villager exclaiming deliriously his good fortune in the first panel: "Je suis riche! Riche! Riche! . . . J'ai . . . J'ai . . ." ("I am rich! Rich! Rich! . . . I . . . I . . ."), and then in the second panel, holding a potted seedling identified as *Takhtajania perrieri,* "J'ai faim . . ." ("I am hungry"). Ironically, *Takhtajania* holds absolutely no value whatsoever for the villagers living in the immediate area. When shown the plant, they had neither a use nor a vernacular name for it. Nevertheless, *Takhtajania* continues to shine prominently on the political landscape, having been chosen as the emblem for Madagascar's exhibit at EXPO-2000 in Hanover, Germany (during the summer of 2000), highlighting the government's conservation and sustainable development programs.

Rediscovery of *Takhtajania* has provided wonderful new research opportunities, the first results of which are reported in the following collection of papers. James Doyle sets the stage by reviewing the fossil history of Winteraceae. Sherwin Carlquist confirms the vesselless nature of *Takhtajania* wood, whereas Taylor Feild and his colleagues examine the condition of vesselless wood from an ecophysiological perspective. Reexamining foliar anatomy, Richard Keating reports mostly brachyparacytic stomata, and thus discounts the original reports of an anomocytic arrangement that contributed to the initial justification of generic status for *Takhtajania*; furthermore, he summarizes a unique nodal anatomy in *Takhtajania.* Peter Endress and his colleagues detail its floral morphology, by virtue of which *Takhtajania* conforms most closely to *Pseudowintera* and *Zygogynum,* in part, due to its small, early-rupturing involucre and apical anther sacs. It was these two features that induced Capuron (1963) to describe the species originally in the genus *Bubbia,* which is now included by some authors in *Zygogynum* s.l. Further exploring the flowers, Andrew Doust examines the ontogeny of perianth parts in Winteraceae. His comparative sequential data suggest that the similarities of an early-rupturing involucre and perianth arrangement exhibited by *Takhtajania* and *Zygogynum* reflect the plesiomorphic state, and that petal fusion in the two genera is non-homologous. His results further imply that the enveloping late-rupturing involucre of *Tasmannia* and *Drimys* has evolved independently in each genus. Delving deeper into the flower, Bruce Sampson reports round or slightly oval apertures in pollen of *Takhtajania,* thus dispelling earlier reports of colpate and trichotomocolpate (trichotomosulcate) apertures; he also finds possible evidence for asynchronous pollen mitosis within a tetrad similar to that in *Drimys* and *Pseudowintera.* Hiroshi Tobe and Bruce Sampson report embryological features indistinct from other Winteraceae, but well distinguished from probable sister Canellaceae. Thierry Deroin's examination of fruit vascular anatomy reveals that the nutritive role is transferred from the median carpellary bundle to the lateral bundles in maturing ovaries during fruit development. At the cytological level, Friedrich Ehrendorfer and M. Lambrou document a "diploidized," possibly paleotetraploid, chromosome number of $2n = 36$, which can only be understood in relation to the paleopolyploidy exhibited by other Winteraceae ($n = 13$ to $n = 43$) by presuming numerous extinction gaps. An analysis of molecular sequence data by Ken Karol and colleagues provides phylogenetic context, firmly placing *Takhtajania* basal and sister to remaining Winteraceae, a result consistent with Leroy's subfamilial designation. Reported elsewhere are studies of the habitat of *Takhtajania* (Birkinshaw et al., 1999b), and an assessment of its risk of extinction (Birkinshaw et al., 1999a). Later this year, Rivolala Andriamparany concludes his studies of the reproductive biology of *Takhtajania perrieri* at the University of Antananarivo under the direction of Elizabeth Rabakonandriana and Len Thien of Tulane University.

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Note added in proof. It happened again! On the very day all of the manuscripts were sent to Allen Press, Madagascar Program coordinator Kendra Sikes and I were looking through backlogged local collector specimens still in their original newspapers collected on the Masoala Peninsula in January, 1996, by Jao Aridy. There was *Takhtajania* in fruit! As before, I immediately dispatched E-mail alert to our Madagascar office, as well as to the Wildlife Conservation Society, who oversees the new Masoala National Park. A successful mission to relocate this new population of *Takhtajania*, which included original collector Jao Aridy and Jean Fortunat Toto of ANGAP/WCS, Rivolala Andriamparany of the University of Antananarivo, and Johny Rabenantoandro of MBG, has now returned from the field. During four days of arduous, wet searching, they found only three plants of *Takhtajania*—one sparsely flowering adult, one sterile adult, and one seedling—located ca. 6 km northeast of Ambanizana (15°34′07″S, 50°00′14″E, or ca. 110 km south of the Anjanaharibe-Sud Special Reserve population) at 790 m altitude on the western slopes of Mt. Ambohitsitondroina. Rivolala Andriamparany, the only member of the team familiar with the Anjanaharibe-Sud population, reports that the flowers of the new population are similar to those he has studied at Anjanaharibe-Sud, but that the leaves and overall habit (smaller, shrubbier) appear somewhat different, confirming my initial impression from the original Jao Aridy collection that the leaves are less thick and coriaceous, and moreover, lack a revolute margin. Along with the significantly lower elevation (790 m vs. 1100–1500 m at Anjanaharibe-Sud), the potential morphological differences tantalizingly suggest the possibility of a second, distinct taxon within *Takhtajania*!